Chapter 1

General Introduction

About elephants

Within the order of *Proboscidea* (Illiger, 1811), the family *Elephantidae* (Gray, 1821) once comprised a total of 26 elephant species within six genera (Shoshani, 1997a). Of these the African elephant (*Loxodonta africana*; Blumenbach, 1797) and the Asian elephant (*Elephas maximus*; Linnaeus, 1758) are the only living representatives. Originally, the African elephant was classed into two subspecies: the Bush or Savanna elephant (*Loxodonta africana africana*) and the Forest elephant (*Loxodonta africana cyclotis*; Matschie, 1900), but this became a matter of debate when recent DNA tests revealed the Forest elephant as a separate species (Roca et al., 2001). The African elephant is the largest living land animal with a shoulder height of 3-4 meters and a weight of 4-7 tons. Apart from its greater size, it differs from the Asian elephant in having larger ears and tusks, a sloping forehead and two "fingers" at the tip of its trunk compared to only one in the Asian species (Shoshani, 1997b). As vegetarians, elephants require much food and spend up to 18 hours feeding each day, consuming a proportional amount of 6-8 percent of their own body weight each day (Sukumar, 1997a). Elephants are also one of the longest-living animal species on earth, although they rarely reach their potential age of 65 years or more in the wild or in captivity (Barnett, 1997; EEG, 2002).

African elephants in the wild and in captivity

African elephants were once abundant in many areas south of the Sahara. By the end of the 20th century, their numbers had dramatically declined, mostly due to uncontrolled ivory hunting, increased cultivation of land and pressures caused by a rapidly expanding human population. Encompassing as much as 7.300.000 km^2 in 1979 (Douglas-Hamilton, 1979), the total home range of the African elephant had decreased by more than 1.5 million km^2 by 1995 (Said et al., 1995). At the same time, the elephant population of the African continent declined from approximately 1.2 million elephants in 1981 to 615.000 individuals in 1995, representing a decrease of 48.9% during that period (Said et al., 1995).

Adult elephant bulls produce the largest tusks and are therefore most threatened. Hunters tend to select mature males to maximise the *per capita* output of hunted ivory, which is reflected in the continued decline of mean tusk size in trade (Luxmoore, 1997). The targeted removal of

adult bulls from the population leads to opportunities for younger males to reproduce, although these may still lack the necessary social competencies and, as a result, experience exceptionally prolonged periods of aggressiveness (Slotow et al., 2000; 2001). Apart from poaching, free-ranging African bulls are also endangered because of consequences of continued and irreversible habitat fragmentation. Shrinking home ranges and persecution force many elephant populations to live in ever smaller, isolated fragments of wild land. On the one hand, this leads to restricted possibilities for bulls in searching for breeding herds. On the other, devastating consequences on the natural habitat cause increased crop-raiding, raiding of food storage containers or increasing use of residential areas by elephants. A persistent elephant-human conflict ensues which has led some African countries to resort to culling to solve the problem. Again, adult elephant bulls are preferred targets because they cause far more damage *per capita* to cultivated land than female herds and seem to be responsible for the majority of accidental deaths, particularly within settlements (Sukumar, 1997b).

At the same time, housing African elephants and, especially males, in zoological gardens, Safari parks or similar institutions is also problematic. Management problems are due to the gender-specific occurrence of increased aggressive behaviour at the onset of sexual maturity combined with the enormous size and strength of an adult bull. The potential risk associated with keeping adult elephant bulls (as also reflected by the regular occurrence of death or severe injury of elephant keepers; www.upali.ch/unfall.html), emphasises the need for highly specialized husbandry and expensive housing. For this reason, relatively few zoological institutions are willing or able to invest in facilities suitable for keeping bulls, leading to a heavily female-biased sex ratio within the captive population. Of the 765 individuals presently held in captivity, only 20% are males and many of these are of a non-breeding age (www.elephant.se/elephant_database.php). The result of this imbalance is a low rate of recruitment (only 48 births have been registered within the last 60 years), leading to a demographically unstable and non-self-sustaining population. Acute management problems with aggressive males can be expected to increase in the next years, when the majority of captive bulls reach sexual maturity. Since ongoing improvements in reproductive management are likely to result in an increased total number of male African elephants in captivity, the management problem is likely to be exacerbated in the longer-term.

The situation of African elephants in captivity and the wild clearly demonstrates that the future of the African elephant is threatened by a variety of factors. In the wild, the rush for ivory has greatly reduced many elephant populations and the continued habitat reduction

leads to increasing numbers of elephant-human conflicts. Elephant bulls are especially affected, either in connection with hunting and tusk size, or in connection with crop raiding, damages of human settlements and human casualties. In captivity, management problems with male elephants reduce the ability to establish a self-sustaining population, with poor prospects for the future since most captive bulls will soon reach an age where aggressiveness and unpredictability in behaviour are set to increase.

Social organisation and reproduction

Among African elephants, pregnancy lasts for about 22 months (630-660 days). In the wild calves are born into a complex elephant society characterised by multi-tiered relationships (Poole, 1994). Female elephants stay in a small, stable social group throughout their lives, made up of an old cow (the matriarch), her adult daughters, their suckling calves, and a number of juvenile and adolescent male and female offspring. Male elephants in the wild leave their natal families at the onset of puberty at about 14 years of age (Moss, 1983; Poole, 1994). At this point in time, adolescent bulls produce fertile sperm and are at least physically able to mate successfully (Hall-Martin, 1987). Bulls henceforth live in a highly dynamic world of changing sexual state, rank, associations, and behaviour, most of the time alone or in small groups of males (so called bachelor groups) in specific bull areas (Poole, 1994; Lee, 1997). Roughly between 21-24 years of age, free-ranging male African elephants begin to show distinct sexually active periods, which are often, but not always associated with a state called “musth”. The word musth is derived from the Urdu, *mast*, meaning intoxicated and represents a behavioural and physiological condition comparable with rutting behaviour in ungulates (Eisenberg et al., 1971; Hall-Martin, 1987; Poole, 1987).

Scientific interest in elephant reproduction was initially focused on female reproductive biology, with important information gathered on the duration of the ovarian cycle, gestation (Brannian et al., 1988; Wasser et al., 1996; Heistermann et al., 1997), and endocrinological changes during conception and pregnancy (Hanks and Short, 1972; Hodges et al., 1983; 1987; 1994; Fieß et al., 1999). In contrast, little is known about male elephant reproduction, although scientific interest in this area has now grown, especially due to the extraordinary manifestations of musth (Jainudeen et al., 1972a; 1972b; Poole and Moss, 1981; Hall-Martin, 1987; Rasmussen et al., 1996; Rasmussen and Schulte, 1998).

The state of musth

The phenomenon of musth was first described in adult Asian bulls in captivity (e.g. Eggeling, 1901). Since the early 1980s it has also been known to occur in adult, male African elephants (Poole and Moss, 1981). The intensity and duration of musth is highly variable and asynchronous between bulls, and even the character of musth within an individual can vary from year to year (Cooper et al., 1990; Poole, 1987; 1994).

Although the precise role of musth in the reproductive context of African elephants is not clear, it has been shown that male elephants in musth leave their normal home ranges, travel long distances and spend significantly less time feeding and resting in order to locate and associate with oestrus females (Hall-Martin, 1987; Poole, 1989b; 1994). It has also been reported that a receptive female will preferably mate with the most dominant bull in the area, which is usually a bull in musth, because a musth bull automatically outranks all bulls in a non-musth condition (Poole, 1989a; 1989b). Females are able to distinguish between musth and non-musth males by detecting musth-male specific chemical olfactory compounds (Rasmussen and Schulte, 1998). Although it is widely accepted that musth plays an important part within the process of reproduction (Rasmussen and Schulte, 1998; Kahl and Armstrong, 2002), the occurrence of the musth condition is not an explicit requirement for male reproductive success since non-musth bulls are also known to mate successfully and have comparable sperm quality (Hall-Martin, 1987; Poole, 1989b; Rasmussen and Schulte, 1998). The characteristics of the sexually active non-musth state and the degree to which it represents an alternative strategy to musth are, however, poorly understood. More information is therefore necessary to understand the functionality of musth and other forms of sexual activity as well as their potential impact on reproduction.

African elephants in musth have a characteristic posture, which is particularly noticeable when they move. The head is carried well above rather than below the shoulder blades and held at such an angle that the chin looks tucked in. The ears are tense and carried high and spread (Poole, 1987; Kahl and Armstrong, 2002). Bulls in musth also repeatedly call at very low frequencies. These musth rumbles are very low pulsating sounds of up to 108 decibels with fundamental frequencies as low as 14 Hz (Poole, 1987; 1994; Poole et al., 1988). Musth is also characterised by an increase in aggression, dominance displays and unpredictability, especially towards other bulls in musth (Jainudeen et al., 1972a; Poole and Moss, 1981; Poole, 1987; Hall-Martin, 1987; Lincoln and Ratnasooriva, 1996). Musth bulls show aggression which overrides normal social male hierarchies (Hall-Martin, 1987). During aggressive interactions, bulls in musth are invariably the winners irrespective of body size, the

factor which normally determines dominance rank between males in the non-musth condition (Poole, 1989a). Apparently, bulls in musth are more likely to be involved in fights, and several musth males have been killed by stronger bulls in musth (Hall-Martin, 1987; Poole, 1994). Furthermore, it is known that the presence of a dominant musth bull can suppress the physical and behavioural changes associated with musth in lower ranking bulls (Poole, 1982).

Asian and African elephants in musth emit further specific signals which notify other male and female elephants of their status. These musth-related signals are mostly characterised by the continuous discharge of urine in a series of discrete drops (urine dribbling) with the penis retained in sheath. This urine has a typical strong odour, especially when associated with a greenish discoloration of the penis and sheath (Moos and Poole, 1981; Poole,1982; 1987; Hall-Martin, 1987). A further visual signal for a bull in musth is the copious secretion from and enlargement of the temporal glands (Jainudeen et al., 1972a; Poole and Moss, 1981; Hall-Martin, 1987; Poole, 1987; Rasmussen and Schulte, 1998), unique modified apocrine sweat glands located just behind the eyes. Among Asian elephants, only bulls in a musth-like condition secrete from these temporal glands. In contrast, both sexes of the African elephant species can produce a more watery form of temporal gland secretion (TGS), which evaporates more quickly and mostly appears under conditions of excitement or stress (Buss et al., 1976; Poole, 1987). Additionally, a second type of TGS was recorded for African elephants in the early 1980s. This type of TGS, produced only by older African bulls in musth, is more sticky, secreted for a longer period of time, and shows several similarities in biochemical composition to the TGS of Asian musth males (Moss and Poole, 1981; Poole, 1987; Rasmussen et al., 1996).

Physiologically, musth in both genera is clearly characterised by a periodic increase in androgen levels (Jainudeen et al., 1972b; Poole et al., 1984; Brannian et al., 1989; Cooper et al.; 1990, Rasmussen et al., 1996). For an Asian elephant in captivity, it was shown that long-term changes in serum concentrations of testosterone are associated with periods of musth (Cooper et al., 1990). In the subsequent years, long-term serum profiles of free-ranging Asian elephants confirmed the association of musth with elevated androgen levels, further demonstrating that bulls over 30 years of age show a clearly defined cyclic pattern in the occurrence of musth (Lincoln and Ratnasooriya, 1996). For the African elephant in contrast, long-term investigations have not been reported for assessing the relationship of endocrinological changes associated with the state of musth. Limited data derived from short-term investigations or cross-sectional studies have confirmed that androgen levels are also significantly higher during the condition of musth than during non-musth (Poole et al., 1984;